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Estimation of Time-Specific Survival Rates from Tag-Resighting Samples: A Generalization of the Jolly-Seber Model

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SUMMARY

The resighting rather than recapturing of individuals that were initially captured, tagged and returned to a population offers a means of circumventing the often traumatic and sometimes fatal effect of repeated capture and handling of wild animals in a tag-recapture study. The behavioral effect of initial capture and tagging, however, must often be accounted for in the model. If sighting records are restricted to tagged individuals, with no attempt at estimating a tagged/untagged ratio in the population, the model requirements are simplified to include only the modeling of mortality among tagged individuals and to exclude recruitment parameters in the unobserved, untagged portion of the population. Short-term capture/tagging effects of specified duration (i.e., lasting for only one time period) are incorporated into the proposed model, and their biasing effects thereby eliminated from estimates of time-specific survival rates. Standard error formulas and tests of the model are provided in this generalization of the Jolly-Seber method of tag-recapture analysis.

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1. Introduction

In many tag-recapture studies, recorded sightings rather than physical recaptures provide the recovery information on animals which have been captured, distinctively tagged and returned to the population. For many species, utilization of sighting rather than recapture records has the obvious practical advantage of greater efficiency. If telescopic or electronic devices are used for field identification of the distinct tags, then there is the more important advantage that tagged animals may be monitored in a relatively undisturbed state. Thus the traumatic and even fatal effect of repeated capture and handling may be avoided. In addition, the possibility of biases due to some tagged animals becoming "trap-happy" or "trap-shy" may be circumvented by the use of sighting records.

Cormack (1964) describes the estimation of time-specific survival rates from sighting records. The well known Jolly-Seber (J-S) method can also be applied to sighting data, as indicated by Jolly (1965). With the correct interpretation, the survival estimators of J-S and Cormack are equivalent.

Both of these models are based on the often unrealistic assumption that tagging has no effect on behavior. However, initial capture and tagging does disturb the animal so new releases may initially have different survival and sighting probabilities than other extant tagged animals. In this situation the J-S estimators of survival will be biased. Robson (1969) considered this problem in the tag-recapture context, and presented a general probability model which allows for an effect of tagging on survival of specified but varying duration. Pollock (1975) extended this model to allow for a tagging effect on "catchability" as well as on

survival. Though potentially useful, these models and the results for estimating population size are presently available only in a cumbersome notational format which deters their application. Cormack (1972), in a more intuitive manner, outlined the estimation of survival rates under Robson's (1969) model, but his treatment does not provide sufficient detail for implementation of the methods (e.g., variance estimators are not given).

We develop here, for the tag and sighting study, a model which allows for a short-term (one period) effect of tagging on survival. Although based on a different interpretation of the sampling process, this model is equivalent to the simplest generalization of the J-S model considered by Robson (1969) and Pollock (1975). Unlike their model formulation, we describe estimation and testing here in the simplest rather than in the most general setting. Our objective is to present a generalization of the J-S model in a readily implemented format which permits estimation of time-specific survival rates in the presence of a tagging effect on survival.

To make interpretation easier, we have used notation which is generally similar to that of Jolly (1965). Use of the methods developed is illustrated with data from a study on migrating sandpipers. Extension of the methods to more complex models is not dealt with here. The interested reader is referred to Brownie and Robson (1980).

2. The Experimental Situation and Notation

2.1 The Experimental Situation

The experimental situation is that described in Cormack (1964). Animals are referred to as birds for convenience. At regularly spaced time intervals, a known number of birds is captured, tagged and returned to the population. These "instantaneous" batch releases are closely followed

(or preceded) by a batch sighting in which the number and identity of only tagged birds is recorded. Tags are unique, so that the capture or sighting history of each individual can be followed separately.

In practice, the sighting operation will usually not be instantaneous, but cover a period of time called the sighting period. The period of survival, or the period to which survival rates apply, is the time between the start of one sighting period and the next. The sighting period should be short in relation to the period of survival. In this context, survival is the complement of mortality plus emigration. It is not possible to distinguish between these two sources of "apparent" mortality.

In this simplest situation the correspondence between the tag and sight data and tag-recapture data should be clear. Note, however, that in order to apply tag and sight models to tag-recapture data there must be no "losses on capture".

More complex situations may arise because the "recovery" of tagged birds and the "trapping" of new birds for tagging are two separate operations. These situations have no analog in the usual tag-recapture context. For example, in trapping new birds for tagging there may be some recaptures of previously tagged birds, so that we have records of recaptures as well as sightings of tagged birds. If capture is assumed to affect behavior, there are numerous possible ways in which such recaptures could be treated. For simplicity, we assume here that such recaptures do not occur.

A second problem arises if the release of newly tagged birds takes place during, or just before, the sighting period. In this case the newly tagged birds are more likely to be sighted unless they immediately disperse. Such sightings of newly marked birds are to be ignored as indicated in

Section 6.1. A third problem arises if the release of marked birds and the sighting period are separated by a substantial time interval, during which mortality may occur. The Jolly-Seber model is not appropriate in this case, as discussed in Section 6.2.

2.2 Notation and Assumptions

The following definitions may be applied in the tag-recapture context by replacing the words "sighted" and "resighted" by "recaptured".

k = the predetermined number of time periods in the study.

N_i = the number of birds tagged and released at time i, $i = 1, \cdots, k-1$.

u_{ij} = the number of birds tagged at time j and <u>first</u> sighted at time i, $j = 1, \cdots, k-1$, $i = j+1, \cdots, k$.

v_{ij} = the number of birds sighted at time j, and next resighted at time i, $j = 2, \cdots, k-1$, $i = j+1, \cdots, k$.

$n_{ij} = u_{ij} + v_{ij}$ = the number of birds tagged or sighted at j and next sighted at i, $j = 2, \cdots, k-1$, $i = j+1, \cdots, k$.

m_i = the total number of tagged birds sighted at time i, $i = 2, \cdots, k$.

V_i = the total number of birds subsequently resighted from the m_i birds sighted at time i, $i = 2, \cdots, k-1$.

U_i = the total number of birds ultimately sighted from the N_i tagged at time i, $i = 1, \cdots, k-1$.

$R_i = U_i + V_i$ = the total number of birds ultimately sighted from the $N_i + m_i$ tagged or sighted at time i, $i = 2, \cdots, k-1$.

Z_i = the number of birds tagged before time i that are not sighted at i, but are sighted after i, $i = 2, \cdots, k-1$.

Note that v_{ij} is undefined for $j = 1$, so let $n_{i1} = u_{i1}$ and $R_1 = U_1$. In symbols,

$$m_i = \begin{cases} u_{21} = n_{21} & i = 2 \\ \sum_{j=1}^{i-1} u_{ij} + \sum_{j=2}^{i-1} v_{ij} = \sum_{j=1}^{i-1} n_{ij} & i = 3, \cdots, k \end{cases},$$

$$V_j = \sum_{i=j+1}^{k} v_{ij} \qquad j = 2, \cdots, 1 , \qquad U_j = \sum_{i=j+1}^{k} u_{ij} \qquad j = 1, \cdots, k-1 ,$$

and

$$Z_i = \begin{cases} U_1 - m_2 & i = 2 \\ Z_{i-1} + U_{i-1} + V_{i-1} - m_i = Z_{i-1} + R_{i-1} - m_i & i = 3, \cdots, k-1 . \end{cases}$$

Definitions of the subtotals m_i, U_i, V_i, and Z_i can be checked by referring to Table 1.

Insert Table 1 here

Two models are considered. The simplest (Model 1) is that of Cormack (1964) and assumes that tagging has no effect on survival. The parameters of this model are

S_i = the probability that a tagged bird alive at time i survives to time i + 1, and

p_i = the probability that a tagged bird alive at time i is sighted at time i .

In the more general model (Model 2) it is assumed that tagging has a one-period effect on survival, so that new releases have a different survival rate S_i^* from that, S_i, of other extant tagged birds.

A basic assumption of the models is that tagged birds behave independently of each other. The population from which tagged birds are drawn

is assumed to be homogeneous with respect to factors which may influence survival such as age or sex. Like Cormack (1964) we assume that the process by which birds are captured for tagging does not provide information about population size or birth parameters. Thus the quantities N_i (the number tagged at time i) are treated as known constants rather than as informative random variables (as in Jolly, 1965). Population sizes and birth rates are not estimable.

For Model 2, the data are represented in an array in Table 1 in a format which is similar to that of Table 1 in Jolly (1965) but, for later purposes, separately recording first sightings and resightings.

The Model 1 representation of the data is equivalent to that of Jolly (1965) and is illustrated in Table 2. Comparison of Tables 1 and 2 should clarify the relationship between our notation and that of Jolly (1965). To further aid the reader who is familiar with Jolly's notation, we list the following similarities and differences:

Brownie and Robson		Jolly
k		ℓ
N_i		n_{i0}
$N_i + m_i$	$n_i = s_i$	(assuming no losses on capture)
m_i		m_i
$u_{il} = n_{il}$		n_{il}
$u_{ij} + v_{ij} = n_{ij}$	n_{ij}	$(j = 2, \cdots, k-1)$
$U_1 = R_1$		R_1
$U_i + V_i = R_i$	R_1	$(i = 2, \cdots, k-1)$
Z_i		Z_i
S_i		ϕ_i
p_i		p_i

In making these comparisons, differences in the experimental situations must

be kept in mind.

Insert Table 2 here

3. Model 2

Model 2 is a generalization of the Jolly-Seber model which is based on the assumption that capture and tagging affect the survival probability of a bird only in the period immediately after release. Except for those birds which are newly tagged, all other birds have the same probability of surviving to the next period. Also, it is assumed that capture and tagging have no effect on subsequent sighting probabilities.

Define S_i^* = probability a bird tagged and released at time i survives to $i+1$, $i = 1, \cdots, k-1$.

S_i = probability a bird tagged before i, and alive at time i, survives to $i+1$, $i = 2, \cdots, k-1$.

$p_i = 1 - q_i$ = probability of being sighted at time i for tagged birds which have survived to i, $i = 2, \cdots, k$.

ρ_i = probability a tagged bird alive at time i is sighted at i or later

$$= \begin{cases} p_i + q_i S_i \rho_{i+1} & i = 2, \cdots, k-1 \\ p_k & i = 2 \end{cases}$$

Part of the chain of events resulting in sightings for the N_1 birds released at time 1 under Model 2 is indicated in Figure 1 below.

Insert Figure 1 here

Recall that if there is some overlap between the release of tagged birds and the sighting period at time i, then any sightings of these new releases are ignored (see Section 6.1), and this possibility is not included in Figure 1.

The likelihood of the data array $\{u_{ij}, v_{ij}\}$ under Model 2 is derived as follows. Note that the entries (u_{ij} or v_{ij}) in any column of the data array in Table 1 correspond to a set of mutually exclusive events. Thus, $(u_{i+1,i}, u_{i+2,i}, \cdots, u_{ki})$ is Multinomial with parameters

$$(N_i, S_i^* p_{i+1}, S_i^* q_{i+1} S_{i+1} p_{i+2}, \cdots, S_i^* q_{i+1} S_{i+1} \cdots q_{k-1} S_{k-1} p_k) \quad ,$$

and for $i = 1, \cdots, k-1$ these vector random variables are mutually independent. Conditional on the value of m_i, the vector $(v_{i+1,i}, v_{i+2,i}, \cdots, v_{ki})$ is also Multinomial with parameters

$$(m_i, S_i p_{i+1}, S_i q_{i+1} S_{i+1} p_{i+2}, \cdots, S_i q_{i+1} S_{i+1} \cdots q_{k-1} S_{k-1} p_k) \quad , \qquad i = 2, \cdots, k-1 \quad .$$

Using an appropriate factorization, the distribution function $P[\{u_{ij}, v_{ij}\}]$ is obtained as a product of conditional multinomial distributions, with parameters as indicated in Table 3 in a format corresponding to that of the data array in Table 1.

Insert Table 3 here

The resulting likelihood function for Model 2 is

$$L_2[\{u_{ij}, v_{ij}\}] = \prod_{i=1}^{k-1} S_i^{*U_i} (1 - S_i^* \rho_{i+1})^{N_i - U_i} p_{i+1}^{m_{i+1}}$$

$$\times \prod_{i=2}^{k-1} q_i^{Z_i} S_i^{Z_i + V_i} (1 - S_i \rho_{i+1})^{m_i - V_i} \quad .$$

Noting that the Z_i are functions of the V_i, U_i and m_i, we can now identify a minimal sufficient statistic for L_2 as

$$\mathcal{S}_2 = \{m_2, m_3, \cdots, m_{k-1}, U_1, U_2, \cdots, U_{k-1}, V_2, V_3, \cdots, V_{k-1}\} \quad .$$

The distribution of $\mathcal{L}_2$ is obtained as a product of conditional Binomial distributions as

$$P[\mathcal{L}_2] = \prod_{i=1}^{k-1} P[U_i|N_i] \times \prod_{i=2}^{k-1} P[m_i|m_i+Z_i]P[V_i|m_i]$$

$$= \prod_{i=1}^{k-1} \binom{N_i}{U_i} (S_i^*\rho_{i+1})^{U_i} (1-S_i^*\rho_{i+1})^{N_i-U_i}$$

$$\times \prod_{i=2}^{k-1} \binom{m_i+Z_i}{m_i} (p_i/\rho_i)^{m_i} (1-[p_i/\rho_i])^{Z_i} \binom{m_i}{V_i} (S_i\rho_{i+1})^{V_i} (1-S_i\rho_{i+1})^{m_i-V_i}$$

--- [1] .

The following maximum likelihood (ML) estimators are easily identified from [1]:

$$\widehat{S_i^*\rho_{i+1}} = U_i/N_i, \qquad i = 1,\cdots,k-1 \ ,$$

$$\widehat{S_i\rho_{i+1}} = V_i/m_i, \qquad i = 2,\cdots,k-1 \ ,$$

$$\widehat{p_i/\rho_i} = m_i/(m_i+Z_i), \qquad i = 2,\cdots,k-1 \ ,$$

and we solve for $\hat{p}_i$, $\hat{S}_i$ and $\hat{S}_i^*$. This gives

$$\hat{p}_i = V_i/(Z_i+V_i), \qquad i = 2,\cdots,k-1 \ ,$$

$$\hat{S}_i = \frac{V_i}{m_i} \frac{m_{i+1}}{V_{i+1}} \frac{Z_{i+1}+V_{i+1}}{m_{i+1}+Z_{i+1}}, \qquad i = 2,\cdots,k-2 \ ,$$

and

$$\hat{S}_i^* = \frac{U_i}{N_i} \frac{m_{i+1}}{V_{i+1}} \frac{Z_{i+1}+V_{i+1}}{m_{i+1}+Z_{i+1}}, \qquad i = 1,\cdots,k-2 \ .$$

Asymptotic variances of these ML estimators obtained, for example, as in Seber (1973), are

$$\mathrm{Var}(\hat{p}_i) = p_i^2\left\{\frac{1}{E(V_i)} - \frac{1}{E(V_i+Z_i)}\right\}, \qquad i = 2,\cdots,k-1 \ ,$$

$$\mathrm{Var}(\hat{S}_i) = S_i^2\left\{\frac{1}{E(V_i)} - \frac{1}{E(m_i)} + \frac{1}{E(V_{i+1})} - \frac{1}{E(m_{i+1}+Z_{i+1})} + \frac{E(V_{i+1}) - E(m_{i+1}+Z_{i+1})}{E(m_{i+1})E(V_{i+1}+Z_{i+1})}\right\}, \qquad i = 2,\cdots,k-2$$

and

$$\mathrm{Var}(\hat{S}_i^*) = S_i^{*2}\left\{\frac{1}{E(U_i)} - \frac{1}{N_i} + \frac{1}{E(V_{i+1})} - \frac{1}{E(m_{i+1}+Z_{i+1})} + \frac{E(V_{i+1}) - E(m_{i+1}+Z_{i+1})}{E(m_{i+1})E(V_{i+1}+Z_{i+1})}\right\}, \qquad i = 1,\cdots,k-2 \ .$$

Non-zero asymptotic covariances are listed in Appendix 1. Estimates of the large-sample variances and covariances are obtained by replacing parameters by their ML estimates, e.g., $E(V_i)$ is replaced by the observed value V_i, and S_i by $\hat{S}_i$, etc.

4. Model 1 and a Test of Model 1 Versus Model 2

4.1 Model 1 and Its Relationship to the Jolly-Seber Model

In order to determine whether capture and tagging effect the survival rate in the period immediately following release, we compare Model 2 with Model 1, which is Cormack's (1964) model and is also essentially the J-S model. Thus, under Model 1 all tagged animals alive at time i, regardless of capture history, have the same probability p_i of being sighted at time i .

Under Model 1 it is not necessary to distinguish between first sightings, or u_{ij}'s, and resightings, or v_{ij}'s . However, the u_{ij}, v_{ij} notation is used in order to facilitate comparison with Model 2. The representation of the data under Model 1 is illustrated in Table 2. Allowing for differences in notation, it can be seen that this is equivalent to the representation in Table 1 of Jolly (1965).

As under Model 2, the likelihood of the data array $\{u_{il}, u_{ij} + v_{ij}, j \geq 2\}$ is obtained as a product of conditional multinomial distributions. These distributions are characterized in Table 4 by exhibiting the size parameters and cell probabilities in a format corresponding to that of the data array in Table 2.

Insert Table 4 here

The likelihood function under Model 1 reduces to

$$L_1\{u_{il}, u_{ij}+v_{ij}, j\geq 2\} = \prod_{i=2}^{k} \left\{ p_i^{m_i} q_i^{Z_i} S_{i-1}^{Z_i+m_i} \right\} \times (1-S_1\rho_2)^{N_1-R_1} \prod_{i=2}^{k-1} (1-S_i\rho_{i+1})^{N_i+m_i-R_i} ,$$

where

$$Z_k \equiv 0 \qquad \text{--- [2]} .$$

Comparison with p. 234 of Jolly (1965) shows that if there are no losses on capture (i.e., $\eta = 1$), then L_1 is the same as L' except for the factor $\left[N_{i0}!/(N_{i0} - n_{i0})!\right] p_i^{n_{i0}} (1 - p_i)^{N_{i0}-n_{i0}}$. This factor, modeling the probability distribution of n_{i0}, does not appear in L_1 because we do not treat n_{i0} (i.e., N_i) as an informative random variable. The reader is referred also to the comments at the end of Section 3.3 of Seber (1965).

A minimal sufficient statistic for [2] is $\mathscr{s}_1 = \{m_2, m_3, \cdots, m_{k-1}, R_1, R_2, \cdots, R_{k-1}\}$, and the distribution of $\mathscr{s}_1$ under Model 1 is

$$P[\mathscr{s}_1] = \binom{N_1}{R_1} (S_1\rho_2)^{R_1} (1-S_1\rho_2)^{N_1-R_1} \times \prod_{i=2}^{k-1} \binom{Z_i+m_i}{m_i} (p_i/\rho_i)^{m_i} (1-[p_i/\rho_i])^{Z_i} \binom{N_i+m_i}{R_i} (S_i\rho_{i+1})^{R_i} (1-S_1\rho_{i+1})^{N_i+m_i-R_i} .$$

This leads to the following ML estimators:

$$\hat{p}_i = \frac{m_i}{m_i + \frac{Z_i(N_i+m_i)}{R_i}}, \qquad i = 2,\cdots,k-1 \ ,$$

$$\hat{S}_i = \frac{R_i}{N_i+m_i}\,\frac{1}{m_{i+1}+Z_{i+1}}\left\{m_{i+1} + \frac{Z_{i+1}(N_{i+1}+m_{i+1})}{R_{i+1}}\right\}, \qquad i = 2,\cdots,k-2 \ ,$$

and

$$\hat{S_{k-1}p_k} = \frac{R_{k-1}}{N_{k-1}+m_{k-1}} \ .$$

Note that, allowing for differences in notation, and assuming no losses on capture, $m_i + Z_i(N_i + m_i)/(R_i)$ is the same as Jolly's $\hat{M}_i$, and the above estimators are identical to the J-S estimators.

For completeness, the asymptotic variances and covariances of these estimators are included in our notation in Appendix 2, but we note that they are equivalent to the corresponding formulas in Jolly (1965).

4.2 Test of Model 1 Versus Model 2

We can now derive a test of the assumption that capture and tagging have no effect on survival and sighting rates, against the alternative that capture and tagging affect survival in the period immediately following release, i.e., a test of Model 1 against Model 2.

The test is based on the conditional distribution under Model 1 of $\mathscr{l}_2$ given $\mathscr{l}_1$ denoted by $P_{M_1}[\mathscr{l}_2|\mathscr{l}_1]$, and given by

$$P_{M_1}[\mathscr{l}_2|\mathscr{l}_1] = \prod_{i=2}^{k-1} \binom{m_i}{V_i}\binom{N_i}{U_i} \Big/ \binom{N_i+m_i}{V_i+U_i} \qquad \text{--- [3]} \ .$$

Each hypergeometric variable in [3] can be approximated by a chi-square variable in the usual way, and a contingency chi-square test on one degree of freedom can be carried out (see Table 5). For $i = 2,\cdots,k-1$, these chi-square statistics are asymptotically independent and may be added to give a total chi-square statistic on k-2 degrees of freedom.

Table 5

Contingency tables for test of Model 1 against Model 2

U_i	$N_i - U_i$	N_i
V_i	$m_i - V_i$	m_i
		$N_i + m_i$

$i = 2,\cdots,k-1$

Rejection of Model 1 in favor of Model 2 would indicate that tagging does affect survival during the period following release. This test has been suggested by Robson (1969) in the tag-recapture context as a test for initial mortality of fish due to tagging (see also Seber, 1973, Table 5.10).

5. Tests of Fit to Models 1 and 2

5.1 Non-discriminant Goodness-of-Fit Tests

For each of the Models 1 and 2 the residual distribution, i.e., the conditional distribution of the data array given the minimal sufficient statistic, is used to obtain a goodness-of-fit test of the model (see also Brownie and Robson, 1976). The derivations of the residual distributions are straightforward and are omitted for brevity. We need the following notation:

$$m^*_{i1} = u_{i1}, \qquad i = 2,\cdots,k \ ,$$

and

$$m^*_{ij} = \sum_{\ell=1}^{j} u_{i\ell} + \sum_{\ell=2}^{j} v_{i\ell}, \qquad \begin{matrix} j = 2,\cdots,k-1 \\ i = j+1,\cdots,k \end{matrix} \ .$$

Note that m^*_{ij} is obtained by summing from left to right across the entries in the $\underline{i}$th row of Table 1 as far as u_{ij}, hence $m^*_{i+1,i} = m_{i+1}$.

Model 1

The residual distribution for Model 1 is

$$P_{M_1}[\{u_{i1}, u_{ij}+v_{ij}, j\geq 2\}|\mathscr{A}_1] = P_{M_1}[\{n_{ij}\}|\mathscr{A}_1]$$

$$= \prod_{i=2}^{k-2} \frac{\binom{R_i}{n_{i+1,i}, \cdots, n_{ki}} \binom{Z_i}{m^*_{i+1,i-1}, \cdots, m^*_{k,i-1}}}{\binom{Z_i+R_i = Z_{i+1}+m_{i+1}}{m_{i+1}, m^*_{i+2,i}, \cdots, m^*_{ki}}} .$$

For $i = 2, \cdots, k-2$, the corresponding contingency tables are

$m^*_{i+1,i-1}$	$n_{i+1,i}$	m_{i+1}
$m^*_{i+2,i-1}$	$n_{i+2,i}$	$m^*_{i+2,i}$
$\vdots$	$\vdots$	$\vdots$
$m^*_{k,i-1}$	n_{ki}	m^*_{ki}
Z_i	R_i	$Z_i + R_i$

,

each yielding a chi-square statistic on $k - i - 1$ degrees of freedom. (If pooling is necessary this should be done by combining rows element by element and reducing the degrees of freedom appropriately.) The chi-squares corresponding to each table are asymptotically independent and may be added to give a total chi-square for the goodness-of-fit test of Model 1.

Model 2

$$P_{M_2}[\{u_{ij}, v_{ij}\} | \mathcal{A}_2]$$

$$= \prod_{i=2}^{k-2} \frac{\binom{U_i}{u_{i+1,i}, \cdots, u_{ki}} \binom{V_i}{v_{i+1,i}, \cdots, v_{ki}} \binom{Z_i}{m^*_{i+1,i-1}, \cdots, m^*_{k,i-1}}}{\binom{Z_{i+1}+m_{i+1}}{m_{i+1}, m^*_{i+2,i}, \cdots, m^*_{k,i}}}$$

with contingency tables

$m^*_{i+1,i-1}$	$v_{i+1,i}$	$u_{i+1,i}$	m_{i+1}
$m^*_{i+2,i-1}$	$v_{i+2,i}$	$u_{i+2,i}$	$m^*_{i+2,i}$
$\vdots$	$\vdots$	$\vdots$	$\vdots$
$m^*_{k,i-1}$	v_{ki}	u_{ki}	$m^*_{k,i}$
Z_i	V_i	U_i	$Z_{i+1}+m_{i+1}$

, $i = 2, \cdots, k-2$.

These are used as described for Model 1, to obtain a goodness-of-fit test to Model 2.

When pooling is necessary, we recommend using these goodness-of-fit tests based on the residual distributions $P_{M_\ell}[\{u_{ij}, v_{ij}\} | \mathcal{A}_\ell]$, rather than the conventional test based on a statistic of the form $X^2 = \Sigma(O - \hat{E})^2/\hat{E}$, where $\hat{E}$ is obtained using ML estimates. When cells are pooled in order to calculate X^2, and $\hat{E}$ is based on the unpooled data, the statistic X^2 does not in general have a central chi-square distribution under the null hypothesis that the model is correct.

5.2 More General Models

If the goodness-of-fit tests result in rejection of Models 1 and 2, there may be several reasons for inadequacy of the models, including heterogeneity of

the population sampled. Another possible reason is that the tagging effect is more extensive than the assumptions of Model 2 permit. The methods of the preceding sections are easily extended to form a series of increasingly general models. For example, a generalization of Model 2 is obtained under the assumption that tagging affects not only survival during the period after release, but also the sighting rate at the start of the following period. A still more general model assumes that the tagging effect extends beyond survival and sighting one period after release to survival in the second period following release. Estimation and testing procedures for models reflecting these assumptions are easily obtained using the methods of Sections 2 and 3, and are described in Brownie and Robson (1980).

6. Practical Considerations

In this section we consider features of practical importance which are peculiar to the tag and sight experimental situation, and have no analog in the conventional tag-recapture context.

6.1 Sightings of New Releases

In theory, the release of newly tagged birds and sightings are assumed to occur simultaneously at time i, $i = 2, \cdots, k-1$, and we have so far ignored the possibility that birds tagged and released at "time i" may be sighted at "time i" . In practice, this is a very real possibility, as sighting will usually follow after the release of tagged birds. If the time between release and sighting is short (as it should be), then newly tagged birds may not have dispersed properly and so will be sighted with higher probability than survivors of previous releases. In this case a different sighting rate (say p_i^*) will apply to these new releases, and the sightings at i of birds released at i (denoted by u_{ii}) will not provide information about p_i, nor about S_i . It is easily proved that the binomial estimator u_{ii}/N_i of p_i^* is independent of

the estimators of all other parameters under Models 1 and 2. It is therefore useless to record the u_{ii} sightings and we do not include them in the data array.

6.2 Release Followed after an Interval by Sighting

For practical reasons, release and sighting may regularly be separated by a time interval which is substantial relative to the period of survival. In this case the assumptions concerning survival and sighting rates must be examined carefully to determine which models are appropriate. We define "time $i+1$" to be the time of the sighting which follows the ith release of tagged birds, $i = 1, \cdots, k-1$. Then the period of survival to which S_i relates is the period between sightings at i and at $i+1$.

Even if tagging has no effect on survival or sighting rates Model 1 will not be appropriate. This is because the survival rate S_i for the period between sightings at i and at $i+1$ will not apply to birds in the ith release in the much shorter period between their release and sighting at $i+1$.

If there is a tagging effect on survival, but the interval between release and the following sighting is long enough for this effect to wear off, and for birds to disperse properly, then Model 2 will be appropriate. If birds do not disperse by the following sighting period or if the tagging effect on survival persists beyond the first sighting period, then more general models are needed.

7. An Example

The methods we have described are applied here to tag and sighting records collected in a study carried out to investigate factors influencing daily emigration rates of semi-palmated sandpipers (Calidris pusilla), migrating from a staging area on the shore of Sibley Lake, North Dakota. Each day, the release of newly tagged birds was followed by a visual survey of the population, and

sightings of previously tagged birds were recorded. There was virtually no mortality during the $2\frac{1}{2}$-month study period, so daily "survival" rates were assumed complementary to the departure or emigration rates.

The researcher questioned the validity of the J-S model (Model 1) for these data, as he felt that the trauma experienced during capture and tagging may have resulted in the premature migration of some birds away from the study area on the day following release. He was prepared, however, to assume that survival (and departure) rates were otherwise unaffected by capture history, hence Model 2 seemed appropriate. Efficient use of the data was essential as numbers tagged were not large, so the comparison of Models 1 and 2 was also important.

For illustrative purposes, only a portion of the data set, corresponding to the 30-day period 7.25.78 to 8.23.78, is used here. Table 6 contains the tagging and sighting records displayed as in Table 1 for Model 2, with first sightings and resightings recorded separately in alternating columns. Records for days 10 to 20 are not displayed. The complete data set will be contained in David Lank's Cornell University Ph.D. thesis.

Insert Table 6 here

The summary statistics used in calculating the Model 2 estimates, and the resulting estimates, are presented in Table 7. Note that $1 - \hat{S}_i$ is the estimated departure rate on day i for birds tagged before i, and $\mathrm{Var}(\hat{S}_i)$ is the estimated variance of $\hat{S}_i$ and of $1 - \hat{S}_i$. As $N_4 = N_9 = 0$, the parameters S_4^* and S_9^* are not estimable. The calculation of $\hat{S}_i$ and $\hat{S}_i^*$ for $i = 8$ (day 8) is illustrated below.

$$\hat{S}_8 = \frac{V_8}{m_8}\frac{m_9}{V_9}\frac{Z_9+V_9}{m_9+Z_9} = 29/31 \times 24/20 \times \frac{132+20}{24+132} = 1.0938$$

and

$$\hat{S}^*_8 = \frac{U_8}{N_8}\frac{m_9}{V_9}\frac{Z_9+V_9}{m_9+Z_9} = 11/20 \times 24/20 \times \frac{132+20}{24+132} = 0.6431 \quad .$$

Insert Table 7 here

The estimate $\hat{S}_8 = 1.09$ illustrates an unappealing small-sample property of the unconstrained ML estimators of survival for many tag-recapture models (i.e., the property that the estimates may exceed 1). For this data set, it is likely that on many days the true survival rates are close to 1, hence it is not surprising that many of the estimates (which are not very precise) are greater than 1. Various methods of adjusting these estimates have been suggested, e.g., Buckland (1980), none of which are entirely satisfactory. In the sandpiper study, such adjustments were not attempted since the relative magnitudes of the estimates were of greater interest than the actual values.

Results for the test of Model 1 versus Model 2 are contained in Table 8. As described in Section 4.2, single degrees of freedom chi-square statistics are obtained from tables of the form

U_i	$N_i - U_i$	N_i
V_i	$m_i - V_i$	m_i
		$N_i + m_i$

; e.g., for i = 10,

90	20	110
27	8	35
		145

,

yielding a chi-square value of 0.37 on 1 degree of freedom. Table 8 contains these chi-square values with the exception of those corresponding to

tables where an expected cell frequency of < 5 occurred. This criterion may be unnecessarily stringent to ensure validity of the chi-square approximation, but it was used because of the additional concern that small cell frequencies would invalidate the assumption of independence among the individual chi-square statistics.

Insert Table 8 here

The total test statistic of 32.26 on 14 degrees of freedom (obtained by summing entries of Table 8) is significant at the 1% level, indicating that Model 2 is preferred to Model 1. Examining the individual values in Table 8 shows, however, that only three of these are "large" (> 3.84, say). Thus for many of the tagging occasions there is little evidence of an immediate effect on survival. With a few exceptions, the J-S (Model 1) survival estimators will probably not be seriously biased, and may be preferred in this situation because of their greater precision.

The validity of Model 2 is assessed by means of the goodness-of-fit test described in Section 5.1. A considerable amount of pooling was necessary to meet the criterion of expected cell frequencies of at least five.

For i = 24, the raw table

31	9	0
39	9	3
20	6	2
21	7	2
12	2	3
13	3	0

, after pooling, gave

70	18	3
66	18	7

with a chi-square value of 1.72 on 2 degrees of freedom. The total test statistic gave a value of 173.57 on 55 degrees of freedom, indicating a poor fit to Model 2.

There are several possible explanations for the inadequacy of Model 2. The study area was a staging site for the sandpipers during the course of

their southward migration. Birds were arriving at and departing from the study area (staging site) during most of the study period. On any day, for a given bird the departure probability may be related to this unknown sojourn time as well as to current or impending weather conditions and other environmental factors. Heterogeneity of departure probabilities induced by this type of "age-dependence" could account for lack of fit to the Model 2 assumption of only "date-dependence". The Model 2 assumption that survival is independent of capture history, except immediately after tagging, might therefore be false. Another possible reason for departure from the Model 2 assumptions (hence also from those of Model 1) is that tagging may have resulted in out-migration from the immediate study area which was temporary and of varying duration, rather than permanent.

Examination of individual contingency tables (not presented here) showed that lack of fit to Model 2 was not generally a serious problem. More complex models would have required additional information and would not have been useful for these data due to the small numbers involved. The Model 2 survival estimates were therefore used to obtain information concerning the effect of factors such as weather patterns on departure rates. This is discussed in Lank's thesis.

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REFERENCES

Brownie, C. and Robson, D. S. (1976). Models allowing for age-dependent survival rates for band return data. Biometrics 32, 305-323.

Brownie, C. and Robson, D. S. (1980). Estimation of time-specific survival rates from tag-resighting samples: A generalization of the Jolly-Seber model. Paper No. BU-725-M in the Biometrics Unit Mimeograph Series, Cornell University, Ithaca, New York, U. S. A.

Buckland, S. T. (1980). A modified analysis of the Jolly-Seber capture-recapture model. Biometrics 36, 419-435.

Cormack, R. M. (1964). Estimates of survival from the sighting of marked animals. Biometrika 51, 429-438.

Cormack, R. M. (1972). The logic of capture-recapture estimates. Biometrics 28, 337-343.

Jolly, G. M. (1965). Explicit estimates from capture-recapture data with both death and immigration - stochastic model. Biometrika 52, 225-247.

Pollock, K. H. (1975). A K-sample tag-recapture model allowing for unequal survival and catchability. Biometrika 62, 577-583.

Robson, D. S. (1969). Mark-recapture methods of population estimation. In New Developments in Survey Sampling, N. L. Johnson and H. Smith, editors, 120-140. New York: Wiley.

Seber, G. A. F. (1965). A note on the multiple-recapture census. Biometrika 52, 249-259.

Seber, G. A. F. (1973). Estimation of Animal Abundance and Related Parameters. London: Griffin.

APPENDIX 1

Non-zero Asymptotic Covariances of the Model 2 Estimators of Survival and Sighting Rates

$$\mathrm{Cov}(\hat{p}_i, \hat{S}_i) = p_i S_i \left\{ \frac{1}{E(V_i)} - \frac{E(m_i + Z_i)}{E(m_i)E(V_i + Z_i)} \right\}, \qquad i = 2, \cdots, k-2 \ ,$$

$$\mathrm{Cov}(\hat{S}_i, \hat{S}_i^*) = S_i S_i^* \left\{ \frac{1}{E(V_{i+1})} - \frac{1}{E(m_{i+1} + Z_{i+1})} + \frac{E(V_{i+1}) - E(m_{i+1} + Z_{i+1})}{E(m_{i+1})E(V_{i+1} + Z_{i+1})} \right\} ,$$

$$i = 2, \cdots, k-2 \ ,$$

$$\mathrm{Cov}(\hat{S}_i^*, \hat{p}_{i+1}) = -S_i^* p_{i+1} \left\{ \frac{1}{E(V_{i+1})} - \frac{1}{E(m_{i+1} + Z_{i+1})} - \frac{E(Z_{i+1})}{E(m_{i+1})E(V_{i+1} + Z_{i+1})} \right\} ,$$

$$i = 1, \cdots, k-2 \ ,$$

$$\mathrm{Cov}(\hat{S}_i, \hat{p}_{i+1}) = -S_i p_{i+1} \left\{ \frac{1}{E(V_{i+1})} - \frac{1}{E(m_{i+1} + Z_{i+1})} - \frac{E(Z_{i+1})}{E(m_{i+1})E(V_{i+1} + Z_{i+1})} \right\},$$

$$i = 2, \cdots, k-2 \ ,$$

$$\mathrm{Cov}(\hat{S}_i, \hat{S}_{i+1}) = -S_i S_{i+1} \left\{ \frac{1}{E(V_{i+1})} - \frac{E(m_{i+1} + Z_{i+1})}{E(m_{i+1})E(V_{i+1} + Z_{i+1})} \right\},$$

$$i = 2, \cdots, k-3 \ ,$$

$$\mathrm{Cov}(\hat{S}_i^*, \hat{S}_{i+1}) = -S_i^* S_{i+1} \left\{ \frac{1}{E(V_{i+1})} - \frac{E(m_{i+1} + Z_{i+1})}{E(m_{i+1})E(V_{i+1} + Z_{i+1})} \right\},$$

$$i = 1, \cdots, k-3 \ .$$

APPENDIX 2

Asymptotic Variances and Non-zero Covariances of the Model 1 or J-S Estimators of Survival and Sighting Rates

$$\mathrm{Var}(\hat{p}_i) = p_i^2 q_i^2 \left\{ \frac{1}{E(R_i)} - \frac{1}{N_i + E(m_i)} + \frac{2}{E(m_i)} \right\}, \qquad i = 2, \cdots, k-1 \ ,$$

$$\mathrm{Var}(\hat{S}_i) = S_i^2 \left\{ \frac{1}{E(R_i)} - \frac{1}{N_i + E(m_i)} + q_{i+1}^2 \left[\frac{1}{E(R_{i+1})} - \frac{1}{N_{i+1} + E(m_{i+1})} \right] \right.$$

$$\left. + \frac{p_{i+1} q_{i+1}}{E(m_{i+1} + Z_{i+1})} \left[S_{i+1} \rho_{i+2} + \frac{1}{S_{i+1} \rho_{i+2}} - 2 \right] \right\}, i = 1, \cdots, k-2 \ ,$$

$$\mathrm{Cov}(\hat{p}_i, \hat{S}_i) = p_1 q_i S_i \left\{ \frac{1}{E(R_i)} - \frac{1}{N_i + E(m_i)} \right\}, \qquad i = 2, \cdots, k-2 \ ,$$

$$\mathrm{Cov}(\hat{S}_i, \hat{S}_{i+1}) = -S_i q_{i+1} S_{i+1} \left\{ \frac{1}{E(R_{i+1})} - \frac{1}{N_{i+1} + E(m_{i+1})} \right\}, \qquad i = 1, \cdots, k-3 \ ,$$

$$\mathrm{Cov}(\hat{p}_{i+1}, \hat{S}_i) = -S_i p_{i+1} q_{i+1}^2 \left\{ \frac{1}{E(R_{i+1})} - \frac{1}{N_{i+1} + E(m_{i+1})} + \frac{1}{E(Z_{i+1})} \right.$$

$$\left. - \frac{E(R_{i+1})}{E(Z_{i+1})[N_{i+1} + E(m_{i+1})]} \right\}, \qquad i = 1, \cdots, k-2 \ ,$$

with

$$R_i \equiv m_i \equiv 0 \ .$$

Table 1

Representation of sighting (u) and resighting (v) data for Model 2 for a study with k = 5 sighting periods

Number of Birds Sighted	Number of Birds Tagged and Released							Row Totals
	N_1		N_2		N_3		N_4	
Time 2	u_{21}							m_2
3	u_{31}	v_{32}	u_{32}					m_3
4	u_{41}	v_{42}	u_{42}	v_{43}	u_{43}			m_4
5	u_{51}	v_{52}	u_{52}	v_{53}	u_{53}	v_{54}	u_{54}	m_5
Col. Totals	U_1	V_2	U_2	V_3	U_3	V_4	U_4	

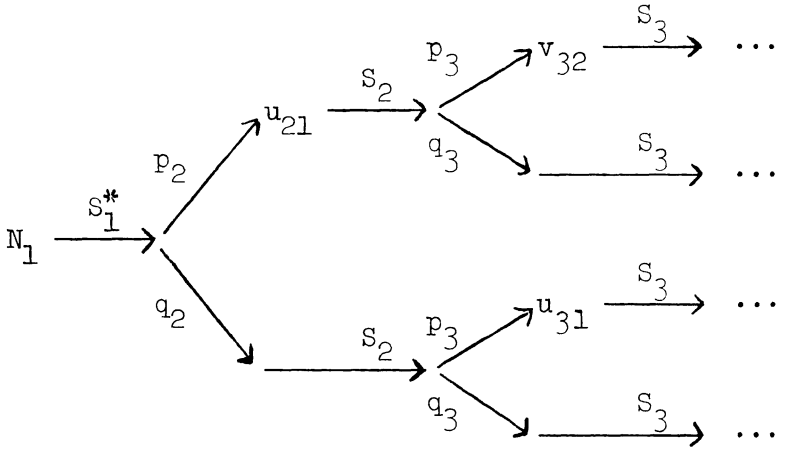

Figure 1

Table 2

Representation of data under Model 1 for a study with $k = 5$

Number of Birds Sighted	Number of Birds Tagged and Released				Row Totals
	N_1	N_2	N_3	N_4	
Time 2	u_{21}				m_2
3	u_{31}	$u_{32} + v_{32} = n_{32}$			m_3
4	u_{41}	$u_{42} + v_{42} = n_{42}$	$u_{43} + v_{43} = n_{43}$		m_4
5	u_{51}	$u_{52} + v_{52} = n_{52}$	$u_{53} + v_{53} = n_{53}$	$u_{54} + v_{54} = n_{54}$	m_5
Col. Totals	$U_1 \equiv R_1$	$U_2 + V_2 = R_2$	$U_3 + V_3 = R_3$	$U_4 + V_4 = R_4$	

Table 3

Parameters of conditional multinomial distributions for Model 2, corresponding to the data array in Table 1

		N_1	m_2	N_2	m_3	N_3
Time	2	$S_1^* p_2$				
	3	$S_1^* q_2 S_2 p_3$	$S_2 p_3$	$S_2^* p_3$		
	4	$S_1^* q_2 S_2 q_3 S_3 p_4$	$S_2 q_3 S_3 p_4$	$S_2^* q_3 S_3 p_4$	$S_3 p_4$	$S_3^* p_4$
Col. totals		$S_1^* \rho_2$	$S_2 \rho_3$	$S_2^* \rho_3$	$S_3 \rho_4$	$S_3^* \rho_4$

Table 4

Parameters of corresponding conditional multinomial distributions

		N_1	$N_2 + m_2$	$N_3 + m_3$	$N_4 + m_4$
Time	2	$S_1 p_2$			
	3	$S_1 q_2 S_2 p_3$	$S_2 p_3$		
	4	$S_1 q_2 S_2 q_3 S_3 p_4$	$S_2 q_3 S_3 p_4$	$S_3 p_4$	
	5	$S_1 q_2 S_2 q_3 S_3 q_4 S_4 p_5$	$S_2 q_3 S_3 q_4 S_4 p_5$	$S_3 q_4 S_4 p_5$	$S_4 p_5$
Col. Totals		$S_1 \rho_2$	$S_2 \rho_3$	$S_3 \rho_4$	$S_4 \rho_5$

Table 6

Tag and sighting records for sandpipers, July 25 to August 23, 1978, Lake Sibley, North Dakota

Time sighted and number sighted	Time tagged and number tagged																															Row totals m_i
	1	2	3	4	5	6	7	8	9	...	21	22	23	24	25	26	27	28	29													
	20	4	64	0	20	9	66	20	0	...	32	38	26	20	19	28	28	31	27													
2	4																															4
3	2	2	1																													5
4	2	1	1	3	2																											9
5	0	0	0	0	8	4	0																									12
6	1	0	0	0	6	0	0	5	1																							13
7	3	0	1	1	8	2	0	2	3	5	3																					28
8	1	0	0	0	1	0	0	0	0	0	2	12	15																			31
9	2	0	0	0	5	0	0	0	2	0	0	3	5	7	0																	24
10	1	0	0	1	4	1	0	1	0	0	1	2	5	5	4	10	0															35
⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮															⋮
21	0	0	0	0	2	0	0	0	1	0	0	1	2	0	0	0	0															78
22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	...	11	10												52
23	0	0	1	0	0	0	0	1	0	0	0	1	1	0	1	0	0	...	8	2	8	5										71
24	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	...	11	2	4	6	15	7								83
25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	...	0	2	6	3	8	2	9	0						40
26	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0	...	6	1	9	4	5	3	9	3	7	1				59
27	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	...	1	2	2	2	3	1	6	2	5	4	13	6		56
28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	...	0	1	3	1	1	1	7	2	5	1	8	3	14	10	71
29	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	...	3	0	1	2	0	1	2	3	1	0	3	5	6	4	23	10	69
30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	...	2	2	0	0	1	0	3	0	3	1	2	3	5	3	13	4	22	11	83
Col. totals	19	4	4	5	53	8	0	11	14	9	8	24	59	29	11	20	0	...	42	22	33	23	33	15	36	10	21	7	26	17	25	17	36	14	22	11	

Table 7

Summary statistics and estimates for tag and sighting records in Table 6

Day	Summary statistics					Parameter estimates					
	N_i	U_i	V_i	m_i	Z_i	$\hat{S}_i$	$1-\hat{S}_i$	$\text{var}(\hat{S}_i)$	$\hat{S}_i^*$	$\text{var}(\hat{S}_i^*)$	$\hat{p}_i$
1	20	19							0.95	0.0024	
2	4	4	4	4	15	1.00	0.00		1.00		0.21
3	64	53	5	5	18	1.11	-0.11	0.0169	0.92	0.0144	0.22
4	0	0	8	9	67	0.96	0.04	0.0195			0.11
5	20	14	11	12	63	1.26	-0.26	0.0663	0.97	0.0516	0.15
6	9	8	9	13	75	0.77	0.23	0.0237	0.99	0.0191	0.11
7	66	59	24	28	64	0.90	0.10	0.0066	0.94	0.0035	0.27
8	20	11	29	31	116	1.09	-0.09	0.0125	0.64	0.0203	0.20
9	0	0	20	24	132	1.02	-0.02	0.0174			0.13
10	110	90	27	35	117	0.89	0.11	0.0095	0.95	0.0049	0.19
11	16	10	48	58	176	1.14	-0.14	0.0247	0.86	0.0390	0.21
12	6	4	19	27	207	0.82	0.18	0.0125	0.77	0.0518	0.08
13	4	4	59	73	157	0.92	0.08	0.0056	1.14	0.0044	0.27
14	4	3	44	52	168	0.98	0.02	0.0075	0.87	0.0663	0.21
15	76	49	39	47	168	1.03	-0.03	0.0101	0.80	0.0080	0.19
16	4	4	43	56	200	0.91	0.09	0.0112	1.18	0.0116	0.18
17	3	1	20	24	223	0.91	0.09	0.0089	0.36	0.0879	0.08
18	29	19	38	42	202	1.31	-0.31	0.0174	0.95	0.0232	0.16
19	34	30	51	85	174	0.96	0.04	0.0207	1.42	0.0368	0.23
20	28	20	30	53	202	0.90	0.10	0.0205	1.14	0.0325	0.13
21	32	22	42	78	174	0.78	0.22	0.0133	1.00	0.0250	0.19
22	38	23	33	52	186	1.15	-0.15	0.0360	1.10	0.0401	0.15
23	26	15	33	71	171	0.84	0.16	0.0225	1.04	0.0478	0.16
24	20	10	36	83	136	0.74	0.26	0.0209	0.85	0.0528	0.21
25	19	7	21	40	142	0.96	0.04	0.0406	0.67	0.0507	0.13
26	28	17	26	59	111	0.79	0.21	0.0270	1.09	0.0532	0.19
27	28	17	25	56	98	0.66	0.34	0.0153	0.90	0.0290	0.20
28	31	14	36	71	69	0.96	0.04	0.0411	0.86	0.0513	0.34
29	27	11	22	69	50	0.32	0.68	0.1036	0.41	0.1729	0.31
30				83							

Table 8

Test of Model 1 versus Model 2

Individual single degrees of freedom chi-squares

i	Chi-square value	i	Chi-square value	i	Chi-square value	i	Chi-square value
10	0.37	20	1.70	24	0.29	28	0.27
15	4.88	21	2.07	25	1.27	29	0.67
18	6.75	22	0.08	26	2.11		
19	8.91	23	0.96	27	1.93		

Total chi-square value = 32.26 with 14 degrees of freedom